

THE FIRST RECORD OF ENDOBIOTIC CORNULITIDS IN A HELIOLITID CORAL FROM THE HIRNANTIAN (LATE ORDOVICIAN) OF ESTONIA

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ABSTRACT – A single specimen of *Stelliporella* sp. (a heliolid coral) from the Hirnantian of Estonia contains at least four specimens of endobiotic cornulitid tubeworm *Conchicolites* sp. The cornulitids settled on the living heliolid colony and were subsequently overgrown by the host coral. The endobiotic cornulitids may have derived significant advantages from inhabiting stable substrates, such as the massive skeletons of corals, which offered both physical support and a reduced risk of dislodgement. The coral skeleton surrounding the *Conchicolites* specimens does not exhibit changes in geometry other than a change in the shape of growth lines above the cornulitid, suggesting a neutral impact on the host and possibly a commensal relationship.

Keywords: bioimmured, tubeworm, tabulate corals, symbiosis, commensalism.

INTRODUCTION

Macroscopic endobiotic polychaete worm symbionts have been frequently observed in modern corals (Hunte *et al.*, 1990a, b; Nishi & Nishihira, 1996, 1999; Hoeksema *et al.*, 2022). In contrast, Paleozoic corals were inhabited by tentaculitoid tubeworms, lophophorates that are unrelated to annelid tubeworms (Darrell & Taylor, 1993; Tapanila, 2004, 2005; Zapalski, 2007; Zapalski *et al.*, 2008; Dixon, 2010; Vinn, 2010; Vinn *et al.*, 2025a). The earliest fossil evidence of symbiotic worms dates back to the Late Ordovician and has been found in rugose (Elias, 1986) and tabulate corals (Tapanila, 2004), preserved as bioclastrations (Palmer & Wilson, 1988; Słowiński *et al.*, 2020). Bioimmured cornulitids (Taylor, 1990) differ from classical bioclastrations in that they have their own biomineralized skeleton. Initially, bioclastrations were considered a result of exclusively commensal interactions (Oekentorp, 1969), but later studies proposed that embedment associations range from parasitic to mutualistic in nature (Stel, 1976; Zapalski, 2007; Vinn *et al.*, 2025c). In contrast, Taylor (2015) challenged the interpretation of endobionts as parasites in fossilized material. He argued that, without conclusive evidence demonstrating the specific costs and benefits of host-symbiont interactions, it is premature to definitively categorize them as parasites. Parasitic relationships, in particular, have a long evolutionary history, dating back to the early Cambrian period (De Baets *et al.*, 2021). This paper defines symbiosis

as any close and enduring biological interaction between two distinct organisms, encompassing mutualistic, commensalistic, or parasitic associations. Modern ecology and biology literature often adhere to De Bary's definition from 1878 or a broader interpretation, which categorizes all forms of interspecific biological interactions as symbiosis. The narrower definition, which limits symbiosis to mutualism alone, is no longer widely accepted (Martin & Schwab, 2013; Robin, 2021).

The Hirnantian is a crucial interval in the evolution of Paleozoic fauna as its time of the end-Ordovician mass extinction (Finnegan *et al.*, 2012; Rasmussen *et al.*, 2019), and data on the symbiotic interactions of that time are therefore especially valuable. The evolutionary paleoecology studies show how ecological interactions evolve and data on symbiosis from the mass extinction interval are equally important to the data on changes of biodiversity. In Baltica, previously endobiotic cornulitids have been described from the Hirnantian stromatoporoids (Vinn *et al.*, 2025b). Endobiotic cornulitids have also been reported from tabulate corals of the Katian and Ludlow of Estonia (Vinn *et al.*, 2012, 2025a). They also occur in the stromatoporoids in the Wenlock of Saaremaa, Estonia (Vinn & Wilson, 2010).

This paper describes in detail the intergrowth between cornulitid tubeworms and *Stelliporella* from the Hirnantian of Estonia having the purposes to discuss the paleoecology of this cornulitid-heliolid association in order to demonstrate the benefits of the associations to tubeworms and analyze the colonization pattern.



GEOLOGICAL BACKGROUND

During the Hirnantian interval, a shallow, warm epicontinental sea covered what is now northern Estonia. In spite of global cooling, the geological record of the Hirnantian in northern and central Estonia is dominated by tropical carbonate rocks due to territories location at very low latitudes, specifically those of the Ärina Formation (Porkuni Regional Stage) (Hints & Meidla, 1997; Hints *et al.*, 2000; Kröger, 2007). A significant climatic shift occurred during the Katian epoch in the Baltica region as the paleocontinent transitioned from a temperate climate zone to a tropical environment and this shift was sufficient to compensate the global cooling in the Hirnantian (Torsvik *et al.*, 2012). Carbonate sedimentation became more prominent during the early stages of warming in the Katian period (Nestor & Einasto, 1997). Faunal groups characteristic of tropical climates, such as tabulate corals and stromatoporoids, first appeared in the early Katian and remained abundant throughout the Hirnantian.

MATERIAL AND METHODS

Seventy-six thin sections of tabulate and heliolitid corals from the collection of the Department of Geology at Tallinn University of Technology (GIT) were examined for the presence

of cornulitids. A single thin section of *Stelliporella* sp. (1/1) from the Porkuni Regional Stage (Hirnantian) contained endobiotic cornulitids. The specimen (GIT 354-104) was collected from Kaomäe Quarry, in central Estonia (Figure 1). The photos originate from the digital photo collection of Department of Geology at Tallinn University of Technology (GIT) available online at <https://geoloogia.info/specimen>. All measurements were obtained using calibrated digital photographs.

RESULTS

A single specimen of *Stelliporella* sp. contains four specimens of *Conchicolites* sp. (Figure 2). The cornulitids have a smooth tube lumen and small diameter characteristic of the genus. The diameters of cornulitid tubes are 0.8 mm, 0.6 mm, 0.4 mm and 0.3 mm, though the final dimensions of the aperture remain unknown but in a single specimen. The tube wall is extremely thin and without obvious structure (Figure 2). The maximum length of the tube is 3.1 mm. The lumen of tubes is filled with translucent calcite. Cornulitid tubes are oriented subparallel to parallel to the coral growth surface. There are no abnormalities in the morphology of the coenenchyme (Figure 2). Cornulitids occur at three different growth stages of the heliolitid colony as identified by growth layers of the coral's skeleton.

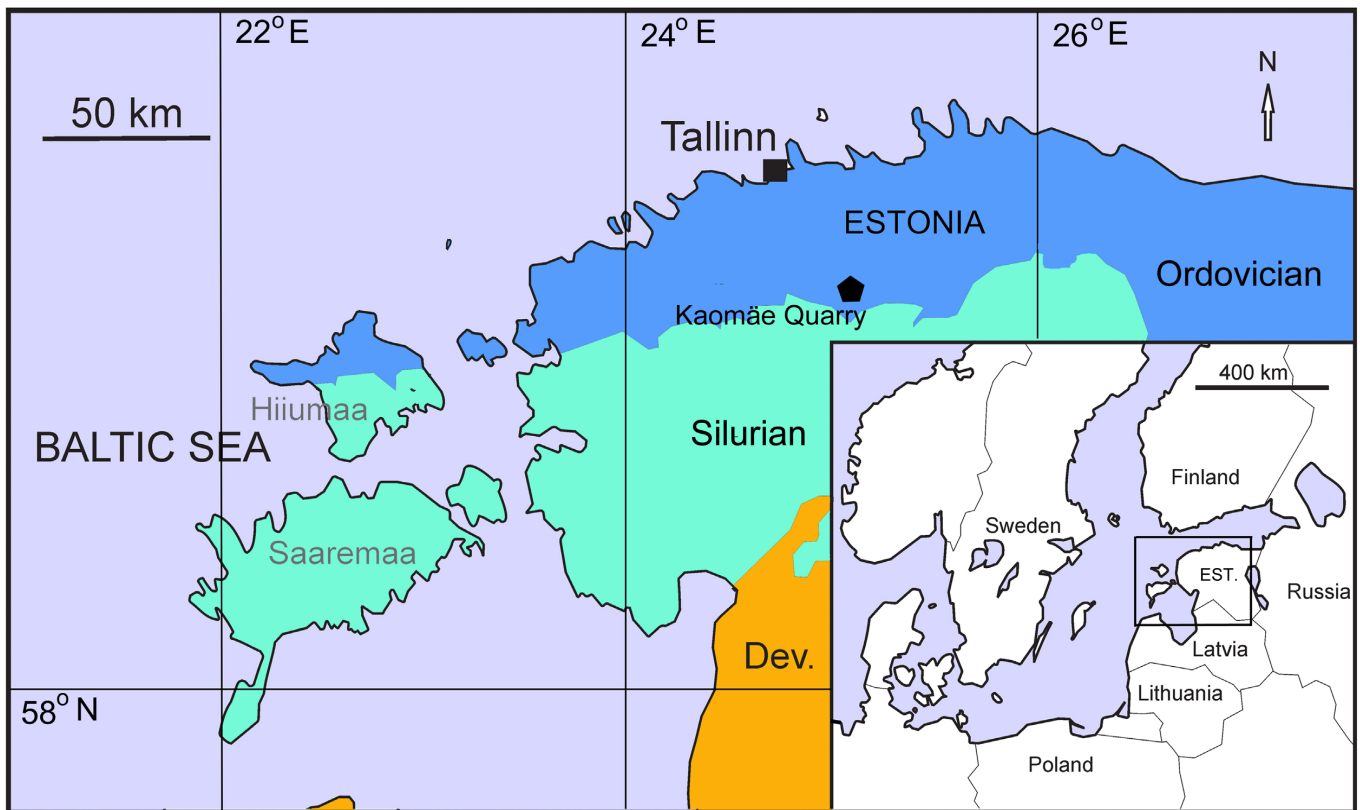


Figure 1. Location of Kaomäe Quarry on geological map.

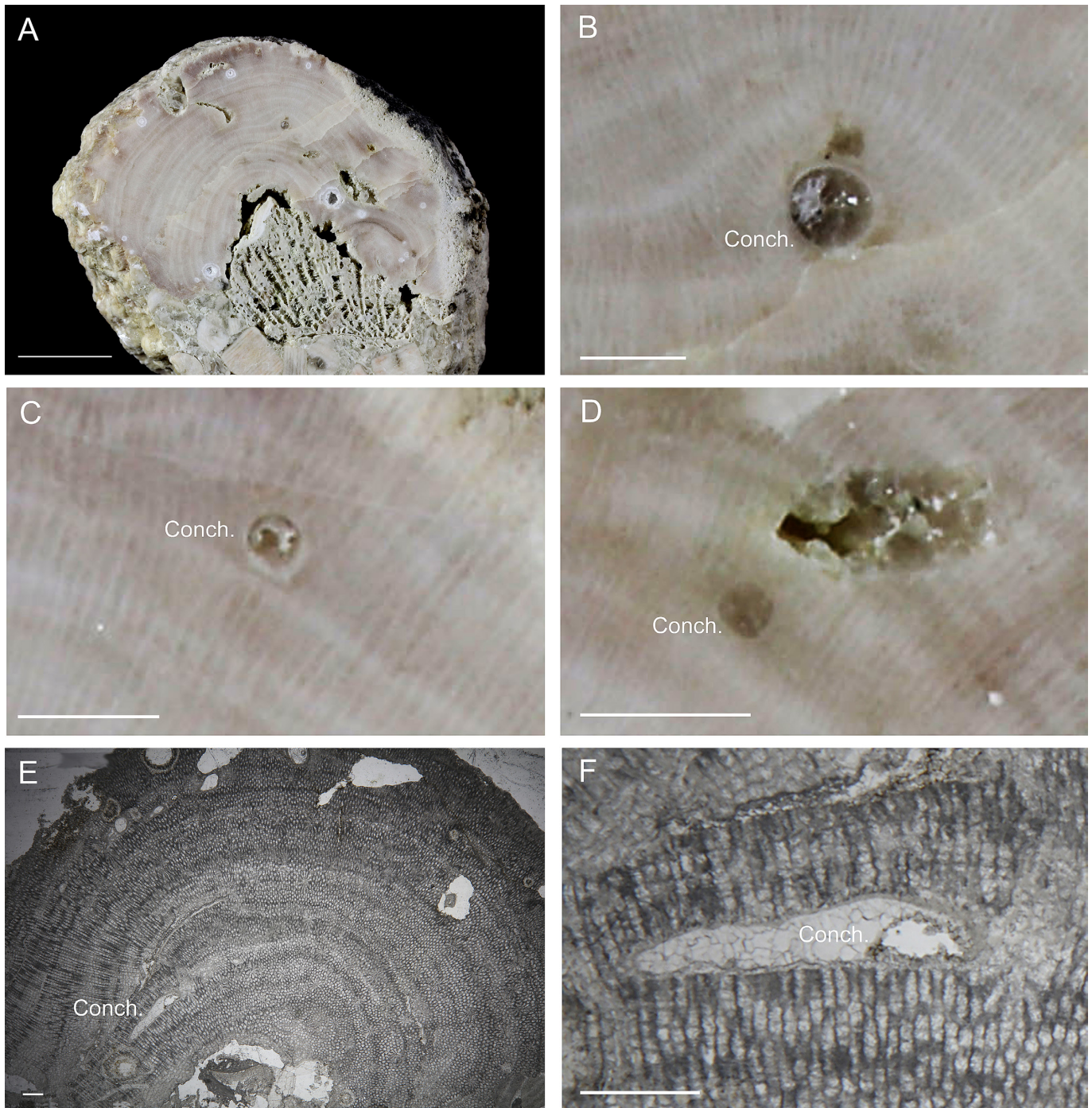


Figure 2. Specimen of *Stelliporella* sp. from the Hirnantian of Estonia containing endobiotic *Conchicolites* sp. (GIT 354-104), collected from Kaomäe Quarry. **A**, section through the tabulate colony. **B–D**, transverse section of endobiotic *Conchicolites* sp. **E–F**, longitudinal section through *Conchicolites* sp.

DISCUSSION

Nature of the association and evolutionary implications

The *syn vivo* nature of embedded cornulitids follows from their complete embedment with the skeleton of the host coral (Tapanila, 2005). The cornulitids must have settled on the living colony of heliolitid and were thereafter fouled by the

host coral (Tapanila, 2005). The *Conchicolites* was oriented nearly parallel to the colony surface, probably because it was growing relatively fast as compared to the host coral. In case of a slower growth rate, one would expect to see vertically oriented cornulitids because such orientation would have allowed it to avoid overgrowth by the host skeleton (Vinn & Wilson, 2010; Vinn & Mõtus, 2012).

Conchicolites possessed a mineralized tube, which likely served as a protective adaptation against predation. However, during the Ordovician, there was a significant increase in predation pressure, particularly from durophagous (shell-crushing) predators (Huntley & Kowalewski, 2007). The earliest evidence of such predatory activity on cornulitids comes from the Katian stage, where signs of unsuccessful predation, such as shell repair following crushing attempts, have been documented (Vinn, 2009). The earliest endobiotic *Conchicolites* also appeared in the Katian possibly as an adaptation to avoid predation (Vinn & Mõtus, 2012). The increase in predation pressure may have played a crucial role in driving the evolution of an endobiotic lifestyle in cornulitids and other related encrusting tentaculitoids (Vinn, 2010; Vinn & Mõtus, 2012). By embedding themselves within living hosts or substrates, these organisms could have gained additional protection from predators, reducing their exposure and increasing survival. Thus, the appearance of endobiontism may represent an evolutionary response to escalating ecological threats in Ordovician marine ecosystems (Vinn, 2009, 2010; Vinn & Mõtus, 2012).

Paleoecological implications

Substrate stability has been proposed as a key factor in the intergrowth between stromatoporoids and rugose corals (Kershaw, 1987). In a similar manner, endobiotic cornulitid symbionts may have also derived significant advantages from inhabiting stable substrates, such as the massive skeletons of corals or stromatoporoids, which offered both physical support and a reduced risk of dislodgement, however, whether there is a trend of cornulitids preferring large substrates such as hardground and corals over small shell should yet to be documented. Many small living substrates such as brachiopods were stabilized via attachment by pedicle. Additionally, occupying a higher tier within the benthic community may have improved access to suspended food particles, further benefiting the suspension-feeding cornulitids (Vinn & Mõtus, 2012).

Studies of modern symbiotic polychaete worms have shown a preference for hosts with strong chemical defenses, such as cnidarians, which protect themselves with stinging cells, that can deter predators (Martin & Britayev, 1998). It is plausible that a similar dynamic existed in Late Ordovician marine ecosystems, with cornulitids selecting hosts that provided not only structural stability but also some degree of protection via its stinging cells. If *Stelliporella* or other host organisms possessed such defenses, they may have served as particularly favorable hosts for endobiotic cornulitids, enhancing the evolutionary persistence of this symbiotic relationship. However, we have a singular example here that does not allow us to draw any firm conclusions. In case most cornulitids were non-symbiotic it would not be proper to attribute too much importance to this occurrence. This association might well represent an accidental embedment that was not related to any major survival strategy. Future studies should show whether cornulitids frequency in corals, or at least heliolitids, was high enough to suspect a survival strategy.

Determining whether the observed symbiotic relationship represents parasitism or mutualism is challenging based on the current material. The coral skeleton surrounding the *Conchicolites* specimens does not exhibit changes in geometry other than changes in the shape of growth lines above the cornulitid. The overall size of tubules in coenenchyme is not significantly reduced either. This may suggest a neutral impact on the host and a commensal relationship (Vinn & Wilson, 2021). In fossil material, clearer signs of parasitism, such as noticeable harm to the host, have been documented, for example, in the case of *Tremichnus* in crinoids (Brett, 1978, 1985).

The presence of *Conchicolites* sp. at various growth stages of the *Stelliporella* sp. colony suggests that colonization by these endobionts occurred repeatedly throughout the coral's development, at least in three separate episodes of colonization during the colony's lifespan. This recurring colonization implies that *Stelliporella* sp. provided a consistently suitable microhabitat for cornulitids and may reflect a long-term ecological relationship between the two organisms. Furthermore, it suggests that the coral's skeletal surface was repeatedly available and accessible to larval settlement by cornulitids, possibly due to interruptions or slower phases in coral growth.

CONCLUSIONS

The discovery of multiple endobiotic *Conchicolites* specimens within a single colony of *Stelliporella* from the Hirnantian of Estonia provides new insights into ancient symbiotic interactions between cornulitids and heliolitid corals. The spatial relationship observed, cornulitids embedded within and subsequently overgrown by the coral host, indicates that these organisms settled during the coral's life and were integrated into its skeletal framework as growth continued. This association implies that *Conchicolites* utilized the stable and elevated substrate offered by coral colonies as a means of securing physical support and minimizing the risk of dislodgement in dynamic marine environments. Notably, the absence of significant morphological alteration in the coral skeleton beyond local modifications of growth lines above the embedded cornulitids indicates a minimal physiological response from the host. This observation supports the interpretation of a commensal relationship, in which the cornulitids benefited from the association without inflicting harm or providing evident benefit to the coral.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

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AUTHOR CONTRIBUTIONS

Olev Vinn: writing – original draft, editing, visualization, investigation, formal analysis, software, resources, data curation.

Olev Vinn, Magdy El Hedeny, Abdullah Alkahtane, Saleh Al Farraj: writing – review. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have used AI-assisted technologies to improve the English of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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